COMMUNICATION DURING CO-ATTENDANCE TIME IN COMMON MURRE (URIA AALGE) PAIRS DURING CHICK REARING

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COMMUNICATION DURING CO-ATTENDANCE TIME IN COMMON MURRE (URIA AALGE) PAIRS DURING CHICK REARING

by

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This thesis is dedicated to both my grandmothers:

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ABSTRACT

The pair co-attendance (time spent together at the nest) of common murres (*Uria aalge*) has been viewed as a component of pair bonding and breeding site maintenance. Alternatively, since a high proportion of co-attendance is spent in the process of role-switching, behaviours exhibited at the nest may also reflect within-pair conflict. In 2009, I examined variations in patterns relating to role-switching (nest interaction sequences) of 17 pairs breeding on Gull Island in Witless Bay, Newfoundland to understand how these variations may reflect intra-pair conflict. Second, I examined two specific behaviours (allopreening and bill-fencing) to investigate how these are related to nest interaction sequence variations and individual quality, as inferred by body condition and corticosterone levels. I also investigated the use of two different recording devices (camcorder and hand-held computer with behavioural research software) to collect field observations. Normally, the returning bird provisions the chick and exchanges brooding duties with its partner which then departs. Sometimes a returning bird has no fish, or, if it does, the mate continues to brood and the returning bird leaves again. The variations from regular nest interaction sequences are considered to be forms of negotiation, in which individuals of the pair negotiate which partner is required to do the energetically costly activity of foraging and which will do the less costly activity of brooding.

Murres allopreened their partners at a higher rate when they returned without a fish to feed the chick compared to partners returning with a fish. Brooding partners that exchanged brooding duties less frequently allopreened at lower rates. These changes in

allopreening rates were associated with extended nest relief times and longer times were associated with higher corticosterone levels. Breeders with better body condition had lower proportions of regular nest interaction sequences. Pair bill-fencing was more prevalent with young chicks (1 to 10 days post-hatch). Finally, in 2009, there were fewer sequences in which the returning bird came without a fish compared to previous years on nearby Great Island when capelin (*Mallotus villosus*) abundance was thought to be higher. In addition, comparison of two different recording devices indicated that extracting data from video recordings made with a camcorder was more accurate than data taken from live observations made using a hand-held computer. Results support the theory that co-attendance may not only be for pair bond maintenance and loafing, but may also be for negotiating brooding duties (the less energetically-costly parental behaviour). Intensive behavioural studies may help to better understand how each individual within a pair communicates their condition and negotiate self-interest in conflicts.

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CHAPTER 1 Introduction and co-authorship statement

1.1 INTRODUCTION

Common murres (*Uria aalge*) are seabirds found in both the North Pacific and Atlantic Oceans. As with many marine birds, murres are long-lived, socially monogamous and have lasting pair bonds. Murres tend to nest on cliffs in high densities in large colonies and show biparental care (Tuck, 1961; Birkhead, 1977, 1980; Nettleship and Evans, 1985; Gaston and Jones, 1998; Ainley, Nettleship, Carter and Storey, 2002). Male and female parents take turns incubating the single egg. When the egg hatches, the chick must be continuously brooded to avoid predation, thus, breeding pairs must alternate brooding activity with foraging to provision the chick (Moody, Wilhelm, Cameron, Walsh and Storey, 2005). Being an obligate single prey-loader, common murres can only provide a single fish for its chick per foraging bout (Bradstreet and Brown, 1985; Harris and Wanless, 1985; 1986; Gaston and Jones, 1998). Pairs of birds typically nest at the same site year after year and raise one chick per breeding season. Once the chick is about 25% of the adult weight (approximately 3 weeks after hatching) it leaves the colony at night for the sea while still flightless. The male parent accompanies it to sea to feed it for 1 to 2 months until it becomes independent (Harris and Birkhead, 1985; Hedgren and Linnman, 1979; Nettleship and Evans, 1985; Ainley et al., 2002).

Murres in the North Atlantic and Pacific Oceans have been studied extensively in the context of response to prey availability (Bryant, Jones and Hipfner, 1999; Zador and Piatt, 1999; Davoren and Montevecchi, 2003; Doody, Wilhelm, McKay, Walsh and

Storey, 2008; Wilhelm, Walsh and Storey, 2008; Burke and Montevecchi, 2009; Evans, Kadin, Olsson and Åkesson, 2013). Breeding adults allocate time at the nest in relation to prey availability. When prey is more readily available, co-attendance (time together at the nest) is higher (Cairns, Bredin and Montevecchi, 1987; Burger and Piatt, 1990; Monaghan, Walton, Wanless, Uttley and Burns, 1994; Uttley, Walton, Monaghan and Austin, 1994; Zador and Piatt, 1999; Wilhelm et al., 2008). In addition, the availability of food in a given year can affect the amount of time mates spend feeding and brooding the chick (Wilhelm, 2004). Although studies have identified general patterns of time allocations for breeding murres, little is known about the details of intra-pair behavioural interactions at the nest.

Pair co-attendance has been previously viewed as a component of pair bonding and breeding site maintenance (Zador and Piatt, 1999; Davoren and Montevecchi, 2003; Lewis, Roberts, Harris, Prigmore and Wanless, 2007). Given that a large proportion of co-attendance time is spent in the process of role switching, an alternative possibility is that the behaviours exhibited during co-attendance partly reflect intra-pair conflict (Wilhelm, 2004). Conflict and pair bonding need not be mutually exclusive. From an evolutionary point of view, conflict can arise because parents have independent interests including maintaining their own individual body condition and promoting future reproductive success. Mutual interests revolve around maintaining the body condition of the partner, because two parents are required for successful reproduction (Jones, Ruxton and Monaghan, 2002).

In biparental species, decreased parental effort by one parent could provoke its mate to work harder and compensate, according to a "graphical model" by Jones et al. (2002). Compensation can be expected for seabirds where elevated predation levels in high density colonies make precise intra-pair coordination of brooding and foraging activities essential. However, there are limits to the level of compensation for individuals and these limits function to maintain biparental care (Jones et al., 2002). The region of conflict lies between "laziness thresholds", the minimum investment that each parent would optimally provide (Jones et al., 2002). According to this model, there is a limit to the exploitation that one individual should impose on its partner (Jones et al., 2002). If this limit is exceeded, the result is the loss of the current breeding attempt, through abandonment by the partner. An individual's ideal level of work is as close to the "laziness threshold" as its partner's body condition allows (Jones et al., 2002). Furthermore, individuals should compensate for their partner only when it is not too costly to do so (e.g., when prey availability is good), or when their partner's condition is marginal, indicating that the partner's reduction in parental care is an honest signal of condition.

An important component of co-attendance in common murre pairs is the process of conducting nest reliefs (Wilhelm, 2004) where partners exchange brooding duties. Research on nest reliefs and nest relief ceremonies in other seabirds suggest that these interactions are an integral part of pair communication (Müller-Schwarze and Müller-Schwarze, 1980; Niebuhr and McFarland, 1983). During co-attendance, a regular nest relief sequence occurs when the male and female are both at the nest simultaneously and

exchange parental duties, whereby the returning partner brings in a fish (the returner) to feed the chick and "relieves" the partner that has been brooding (the brooder). The brooder then departs to bathe and forage (Burger, 1997).

Though a regular nest relief sequence is the most common sequence, there are situations when the brooding mate does not exchange brooding duties, including when: the returning partner does not arrive with a fish, a "relieved" mate does not immediately depart, or if there are multiple nest reliefs before one of the birds leaves the nest site (Storey, Walsh, Doody and Wilhelm, 2007). These behaviours may be considered *nest negotiation* and may indicate that each bird is communicating to honestly signal body condition and quality to their partner (Jones et al., 2002). During nest negotiation, the individuals within the pair may negotiate between brooding duties or the more costly foraging duties, as murre resting metabolic rate is approximately half which includes energetically expensive activities such as diving (Croll and McLaren, 1993) and flying. For murres, flight is energetically costly due to high wing-loading (Gabrielsen, 1996 as cited in Doody et al., 2008) that results from the evolutionary trade-off between diving and flight for alcids (Thaxter, Wanless, Daunt, Harris, Benvenuti, Watanuki, Grémillet and Hamer, 2010).

According to Jones et al. (2002), the amount of conflict in the pair can be predicted by the quality of each individual and to the relative disparity in quality between them. Neither partner can have "perfect" knowledge about the other bird's body condition, so partners must "err on the side of caution" when making parental care decisions such as when to return to the nest (Jones et al. 2002). These actions might

reduce the "region of conflict" (between the parents) as predicted in the model and, therefore, it would be in the best interest of the brooder to communicate its body condition to its returning partner (Jones et al., 2002). The returner, while away, has control of nest activities rather than the brooder, as the returner can decide when to return to the nest site (Jones et al., 2002). However, the brooder has control of when or whether the nest relief will occur once the returner has arrived. Information exchanged will then help the current brooder "estimate" the time it should be absent from the nest for foraging (Jones et al., 2002). More cooperation is anticipated when environmental conditions are poor, or when the body condition is poor for one or both birds (Jones et al. 2002). However, there is the possibility that an individual will be dishonest about its own condition, thus giving this individual an advantage if the partner believes that its condition is worse than it is. The returner could achieve this advantage by arriving back at the nest site to incubate soon after the last nest relief, without first bringing a fish to the chick. However, these strategies are limited by the risk of abandonment of the nest by the partner, which would lead to breeding failure for both parents (Jones et al., 2002). Therefore, there is a trade-off between risk of abandonment and the energetic benefits an individual gains by misleading its partner. Because breeding failure has a large negative influence on fitness, cooperation between mates should be common and dishonest signals should be rare. Further, considering the time and effort it takes to find and court a new mate, it is highly advantageous for individuals in long-lived monogamous species to help maintain the body condition of their partner (Mock and Fujioka, 1990; Fowler, 1995; Jones et al., 2002). When individual common murres persist in making insufficient parental care contributions, their highly parental partners sometimes re-mate if a highly-

parental widowed neighbour becomes available (better option hypothesis; Moody et al., 2005).

Allopreening and bill-fencing are two behaviours that occur during co-attendance. Allopreening is a common behaviour among various bird species in which one bird preens another individual's plumage (Harrison, 1965). Cullen (1963) suggested the term "allopreening", as the behaviour is directed at another individual and has many potential functions such as reciprocity for the maintenance of altruism (Trivers, 1971), parasite removal, maintenance of feathers, mate choice, pair-bond maintenance, stress reduction and parental care stimulation (Kober and Gaston, 2003; Lewis et al., 2007).

Bill-fencing between individuals of a pair is a common behaviour for common murres (93% of interactions observed on Skomer Island; Birkhead, 1978). This behaviour may function as a greeting when the returnee arrives at the nest site (Birkhead, 1978). However, because bill-fencing occurs in seemingly aggressive displays in between mated pairs of other species (Moynihan and Hall, 1954), it is possible that this behavioural pattern may be an important component of communication in conflict situations; this has not been investigated to date and further examination is warranted to better understand its function.

This thesis examines the behaviours that pair members exhibit at the nest site during co-attendance, and how these behaviours are related to individual condition, parental investment and the local ecological conditions in Witless Bay, Newfoundland (Figure 1.1). In Chapter 2, I examine nest interaction sequences and how variation in

these sequences may be related to intra-pair conflict on Gull Island, Witless Bay in 2009. Second, I investigate communication intra-pairs by quantifying the frequency of behaviours such as allopreening and bill-fencing and how these frequencies are related to nest interaction sequences and local food availability. Third, I examine communication patterns within pairs from the perspective of the brooder and returner and in the context of individual quality as measured by corticosterone levels and body condition. In Chapter 3, I investigate nest relief and nest interaction sequences in relation to varying food availability over multiple years in Witless Bay. In Chapter 4, I summarize my findings on behaviours exhibited during co-attendance, the role of behaviours at the nest and suggest future research directions.

1.2 LITERATURE CITED

Ainley, D.G., Nettleship, D.N., Carter, H.R. and Storey, A.E. 2002. Common murre (*Uria aalge*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/666.

Birkhead, T.R. 1977. The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). *Journal of Animal Ecology* 46: 751-764.

Birkhead, T.R. 1978. Behavioral adaptations to high density breeding in the common guillemot *Uria aalge*. *Animal Behaviour* 26: 321-331.

Birkhead, T.R. 1980.Timing of breeding of common guillemots *Uria aalge* at Skomer Island, Wales. *Ornis Scandinavica* 11: 142-145.

Bradstreet M.S.W., Brown, R.G.B. (1985) Feeding ecology of the Atlantic Alcidae. In: Nettleship DN, Birkhead TR (Eds.) The Atlantic Alcidae: the evolution, distribution and biology of the auks inhabiting the Atlantic Ocean and adjacent water areas. Academic Press, London, p 263–318.

Bryant, R., Jones, I.L. and Hipfner, J.M. 1999. Responses to changes in prey availability by common murres and thick-billed murres at the Gannet Islands, Labrador. *Canadian Journal of Zoology* 77: 1278-1287.

Burger, A.E. 1997. Arrival and departure behavior of common murres at colonies: Evidence for an information halo? *Colonial Waterbirds* 20: 55-65.

Burger, A.E. and Piatt, J.F. 1990. Flexible time budgets in breeding common murres: Buffers against variable prey abundance. *Studies in Avian Biology* 14: 71-83.

Burke, C.M. and Montevecchi, W.A. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology* 278: 354-361.

Cairns, D.K., Bredin, K.A. and Montevecchi, W.A. 1987. Activity budgets and foraging ranges of breeding common murres. *Auk* 104: 218-224.

Croll, D.A. and McLaren. E. 1993. Diving metabolism and thermoregulation in common and thick-billed murres. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 163: 160-166.

Cullen, J.M. 1963. Allo-, auto-, and heteropreening. *Ibis* 105: 121.

Davoren, G.K. and Montevecchi, W.A. 2003. Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres *Uria aalge*. *Journal of Avian Biology* 34: 44-53.

Doody, L.M., Wilhelm, S.I., McKay, D.W., Walsh, C.J. and Storey, A.E. 2008. The effects of variable foraging conditions on common murre (*Uria aalge*) corticosterone concentrations and parental provisioning. *Hormones and Behavior* 53: 140-148.

Evans, T., Kadin, M., Olsson, O., and Åkesson, S. 2013. Foraging behaviour of common murres in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices. *Marine Ecology Progress Series* 475: 277–289.

Fowler, G.S. 1995. Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. *American Zoology* 35:318–328.

Gabrielsen, G.W. (1996) Energy expenditure of breeding common murres, p. 49-58. In: W. A. Montevecchi [ed.], Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems. Canadian Wildlife Service Occasional Paper Number 91, Ottawa.

Gaston, A.J. and Jones, I.J. 1998. *The Auks*. Oxford Univ. Press, Oxford.

Harris M.P., Birkhead, T.R. (1985) Breeding ecology of the Atlantic Alcidae. In: Nettleship DN, Birkhead TR (Eds.) Atlantic Alcidae. Academic Press, New York, pp 155–204.

Harris, M.P. and Wanless, S. 1985. Fish fed to young guillemots, *Uria aalge*, and used in display on the Isle of May, Scotland. *Journal of Zoology* 207: 441-458.

Harris, M.P. and Wanless, S. 1986. The food of young razorbills on the Isle of May and a comparison with that of young guillemots and puffins. *Ornis Scandinavica* 17: 41-46.

Harrison, C. 1965 Allopreening as agonistic behaviour. *Behaviour* 24: 161-209.

Hedgren, S., and Linnman, Å. 1979. Growth of guillemot *Uria aalge* chicks in relation to time of hatching. *Ornis Scandinavica* 29-36.

Jones, K.M., Ruxton, G.D. and Monaghan, P. 2002. Model parents: Is full compensation for reduced partner nest attendance compatible with stable biparental care? *Behavioral Ecology* 13: 838-843.

Kober, K. and Gaston, A.J. 2003. Social interactions among breeding Brünnich's guillemots *Uria lomvia* suggest constraints in relation to offspring vulnerability. *Ibis* 145: 413-418.

Lewis, S., Roberts, G., Harris, M.P., Prigmore, C. and Wanless, S. 2007. Fitness increases with partner and neighbour allopreening. *Biology Letters* 3: 386-389.

Mock, D.W. and Fujioka, M. 1990. Monogamy and long-term pair bonding in vertebrates. *Trends in Ecology and Evolution* 5: 39-43.

Monaghan, P., Walton, P., Wanless, S., Uttley, J.D. and Burns, M.D. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis* 136: 214-222.

Moody, A.T., Wilhelm, S.I., Cameron, M.L., Walsh, C.J. and Storey, A.E. 2005. Divorce in common murres: Relationship to assessment of parental quality. *Behavioural Ecology & Sociobiology* 57: 224-230.

Moynihan, M. and Hall, M.F. 1954. Hostile, sexual, and other social behaviour patterns of the spice finch (*Lonchura punctulata*) in captivity. *Behaviour* 7: 33-76.

Müller-Schwarze, D. and Müller-Schwarze, C. 1980. Display rate and speed of nest relief in Antarctic pygoscelid penguins. *Auk* 97: 825-831.

Nettleship, D.N. and Evans, P.G.H. 1985. *Distribution and status of the Atlantic Alcidae.* Pages 53–154 in T. R. Birkhead, and D. N. Nettleship, editors. The Atlantic Alcidae. Academic, London, United Kingdom.

Niebuhr, V. and Mcfarland, D. 1983. Nest-relief behavior in the herring gull. *Animal Behaviour* 31: 701-707.

Storey, A.E., Walsh, C.J., Doody, L.M. and Wilhelm, S.I. 2007. Negotiation: How common murres 'ask' their mates to provide more parental care. Paper presented at the meeting of the Animal Behavior Society, Burlington VT, July.

Thaxter, C.B.,Wanless, S., Daunt, F., Harris, M.P., Benvenuti, S., Watanuki, Y., Grémillet, D. and Hamer, K.C. 2010. Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills. *Journal of Experimental Biology* 213: 1018-1025.

Trivers, R. L. 1971. Evolution of reciprocal altruism. Quarterly Review of Biology. 46: 35-57.

Tuck, L.M. 1961. The murres: their distribution, populations and biology - a study of the genus *Uria*. Canadian Wildlife Service, Ottawa

Uttley, J.D., Walton, P., Monaghan, P. and Austin, G. 1994. The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria-aalge*. *Ibis* 136: 205-213.

Wilhelm, S.I. 2004. Behavioural and physiological responses of breeding common murres (*Uria aalge*): Exploring inter-annual variability within individuals. Ph.D. dissertation, Memorial University of Newfoundland, St.John's.

Wilhelm, S.I., Walsh, C.J. and Storey, A.E. 2008. Time budgets of common murres vary in relation to changes in inshore capelin availability. *Condor* 110: 316-324.

Zador, S.G. and Piatt, J.F. 1999. Time-budgets of common murres at a declining and increasing colony in Alaska. *Condor* 101: 149-152.

1.3 CO-AUTHORSHIP STATEMENT

This research was conducted under the guidance of my co-supervisors, Dr. Anne Storey and Dr. Carolyn Walsh. The field data from Gull Island, Witless Bay, Newfoundland (2008 and 2009) was collected by me or under my supervision. I completed the PCR analysis under the supervision of Drs. Elizabeth Perry and Ed Yaskowiak in the laboratory. The CORT analyses were conducted by Lesley Doody, Amy-Lee Kouwenberg and Megan Rector under the supervision of Dr. Donald McKay. Field data from 1999 and 2000 taken on Great Island, Witless Bay, Newfoundland was collected by Dr. Anne Storey's previous graduate students (Maureen Cameron-MacMillan, Dr. Carolyn Walsh and Dr. Sabina Wilhelm) and assistants. The compiled data from Great Island was provided to me for comparison with Gull Island by Dr. Anne Storey. I was responsible for the data analysis and the development and writing of all chapters. My committee members (Drs. Anne Storey, Carolyn Walsh and Sabina Wilhelm) offered comments and suggestions on the chapters that were incorporated into the thesis prior to submission. Drs. Anne Storey and Carolyn Walsh are co-authors on manuscripts arising from this thesis, and for their financial, fieldwork and intellectual support. Dr. Sabina Wilhelm will also be a co-author due to her intellectual contributions and her contribution of important data in chapter 3.

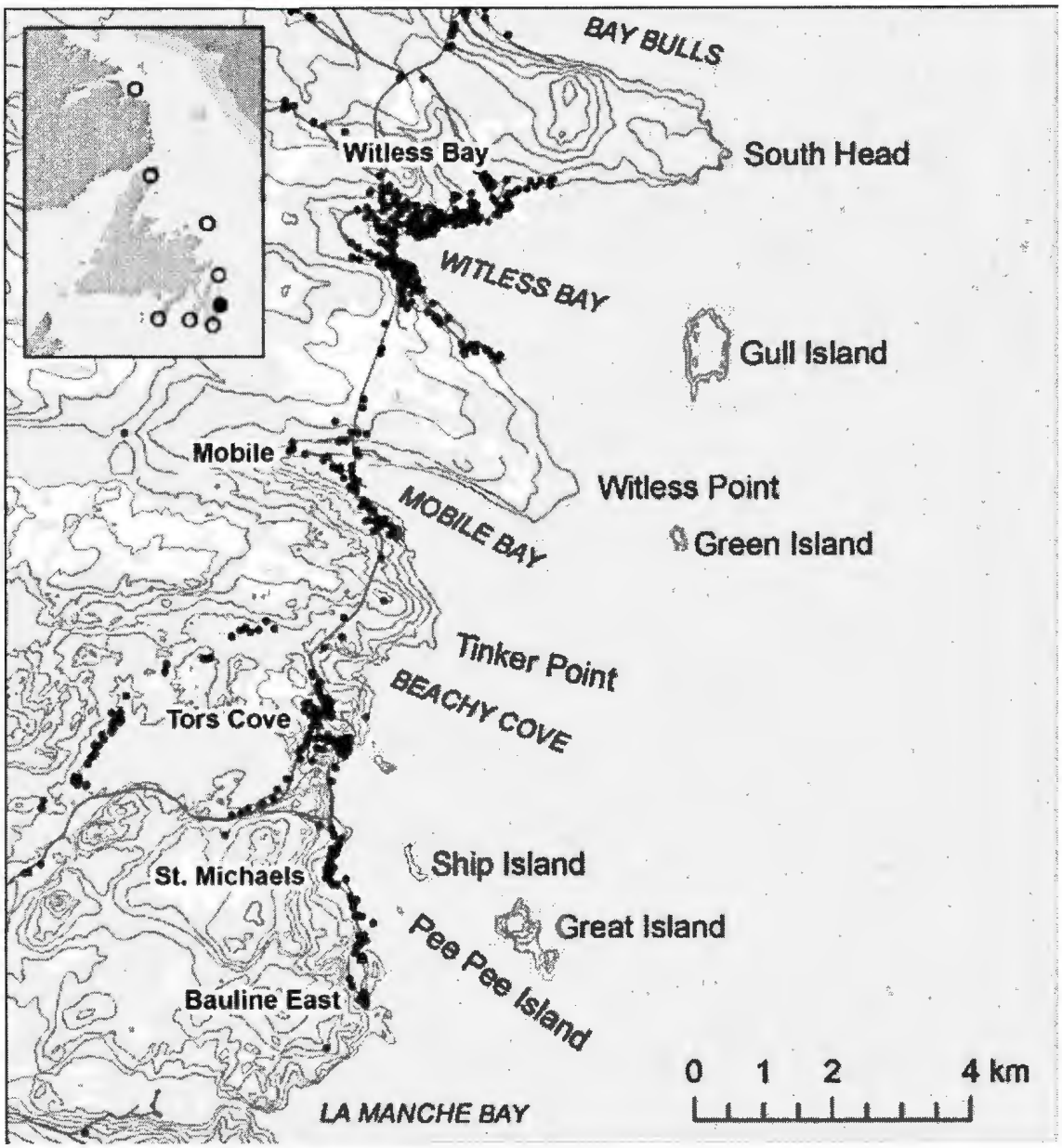

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Figure 1.1 Locations of islands in Witless Bay Ecological Reserve, Newfoundland with common murre breeding pairs in this study.

CHAPTER 2 Intra-pair communication by breeding common murres via nest interactions and co-attendance behaviours

2.1 ABSTRACT

The time that common murre (*Uria aalge*) breeding pairs spend together at the colony (co-attendance) is usually described as pair bonding and social loafing. However, this may also be a time for negotiating parental duties within the pair; namely, the energetically costly activity of foraging and the less costly behaviour of brooding the chick. In a regular nest relief sequence, the returning bird (returner), provisions the chick and takes over brooding duties from its partner (brooder) that then departs. However, sometimes there are sequence variations including no exchange of parental duties, the partner returns without a fish, or there are multiple nest reliefs at the nest site before a bird leaves. I observed 313 nest interaction sequences within 17 breeding pairs on Gull Island, Witless Bay, Newfoundland (2009) to determine how variations from the regular nest relief sequence could provide a way to examine intra-pair interactions that may reflect negotiations. I examined two common behaviours exchanged within pairs, allopreening and bill-fencing, and assessed how these behaviours differed in relation to a regular nest relief sequence, sequence variations and individual quality (inferred by corticosterone levels and body condition). Returners and brooders with high corticosterone levels took longer to begin allopreening. The number and the rate of allopreening bouts for both returners and brooders differed among the various sequence types. Generally, in sequences where no fish was brought in, there was more allopreening by both birds. There was no difference in allopreening behaviours between

returners and brooders during regular nest relief sequences. There were more incidents of bill-fencing in sequences where there were multiple nest reliefs before a bird departed. Also, for pairs in which the body condition of one partner was known, there was a higher proportion of regular nest reliefs when that individual was in poor body condition compared to when the known individual was in better condition. Finally, there was a higher proportion of sequences in which the provisioner in good condition departed again rather than brooded. These differences in the onset, duration and frequencies of various behaviours over different sequence types suggest that allopreening may allow pair members to communicate their physiological status and negotiate behavioural duties to reflect their own self-interest.

2.2 INTRODUCTION

Common murres are philopatric, long-lived seabirds that form monogamous pair bonds and breed on cliffs in high density colonies (Nettleship and Evans, 1985; Gaston and Jones, 1998; Ainley, et al., 2002). Murres show biparental care, with male and female parents taking turns incubating the egg and then feeding and brooding the chick, and successful breeders producing one chick per year (Wanless and Harris, 1986). To prevent predation and help regulate body temperature, one parent continuously broods while the other parent is away foraging to provision the chick (Moody et al., 2005).

Previous work on time budgets of murres suggests that breeding adults allocate time at the nest in relation to availability of prey. When prey was more available, pairs spent more time together at the nest (Cairns et al., 1987; Burger and Piatt, 1990; Monaghan et al., 1994; Uttley et al., 1994; Zador and Piatt, 1999; Wilhelm et al., 2008). This time together, known as co-attendance has been previously described as a component of pair bonding, loafing and breeding site maintenance (Zador and Piatt, 1999; Davoren and Montevecchi, 2003; Lewis et al., 2007). Co-attendance may be the only time that mated pairs spend together during their reproductive years. Therefore, pair performance during co-attendance may be important for each individual's current and future reproductive output by providing a means for individuals to communicate and transfer information about their own physiological condition.

During co-attendance, an exchange of parental duties normally occurs, whereby the returning bird (the returner), which has arrived with a fish, feeds the chick and takes over brooding duties from its partner (the brooder). The brooder then leaves the nest site to bathe, self-provision and forage for the next fish (hereafter "regular nest relief sequence"; Burger, 1997; Ricklefs, 1983). However, regular nest relief sequences do not always occur and behavioural differences during these other sequences have not been investigated to date. When the regular nest relief sequence does not occur, various behaviours may be observed, such as: the mates do not exchange parental duties; the partner returns without a fish; or there are multiple nest reliefs (more than one exchange of brooding duties) before a bird leaves the nest site (Storey et al., 2007). Such variations on the regular nest relief sequence may be forms of *negotiation*, in that they either delay the exchange of brooding duties (possibly to the next co-attendance time) or are counterproductive to provisioning the chick. These exchange types could provide a means for partners to signal to each other information about their current physiological state (e.g., body condition). The information contained in such behaviours may also indicate an individual's quality, and allow partners to assess short and long-term reproductive potential of their mate.

Negotiation of brooding duties is related to energy costs associated with parental care duties and individual quality. Brooding is likely less energetically taxing compared to foraging, as the resting metabolic rate is approximately half of diving (Croll and McLaren, 1993). Furthermore, for alcids, flight is energetically costly due to high wing-loading (Birt-Friesen, Montevecchi, Cairns and Macko, 1989; Gabrielsen, 1996 as cited

in Doody et al., 2008; Gaston, 2004). Therefore, the division of parental care duties may lead to intra-pair conflict. Negotiating partners may show different patterns of behaviours, depending on whether they are attempting to remain a brooder, or become the brooder without having provisioned the chick. Ultimately, the pair has a mutual interest to successfully raise their chick. However, conflict between parents exists when an individual's current body condition or future reproductive success is potentially decreased because it is forced by its partner's low investment to put too much in the current reproductive effort (Houston, Székely and McNamara, 2005; Saraux, Chiaradia, Le Maho and Ropert-Coudert, 2011). Because future reproductive success in murres is often dependent on keeping the same partner (Moody et al., 2005), maintaining the partner's body condition is thus also advantageous for individuals in many long-lived monogamous species (Mock and Fujioka, 1990; Fowler, 1995; Jones et al., 2002, Moody et al., 2005). Despite the conflict, it may be mutually beneficial for a pair to negotiate with each other.

Corticosterone (CORT) is a "stress" hormone and the primary mediator of allostasis (McEwen and Wingfield, 2003). Increased CORT can allow organisms to cope with an "emergency" life history stage (Wingfield, Maney, Breuner, Jacobs, Lynn, Ramenofsky and Richardson, 1998). CORT in relation to chick provisioning rate can also be used as an indicator of individual quality (Doody et al., 2008). Periods of low food availability can negatively influence a breeder's body condition (Weimerskirch, Zimmermann and Prince, 2001) where as food availability decreases or is unreliable, stress hormone levels increase (Kitaysky, Wingfield and Piatt, 1999; Vleck, Vertalino, Vleck and Bucher, 2000; Reneerkens, Piersma and Ramenofsky, 2002; Clinchy, Zanette,

Boonstra, Wingfield and Smith, 2004). Also, when environmental changes caused CORT levels to increase, seabirds in poor body condition increased their self-feeding rather than provisioning their young (Angelier, Clément-Chastel, Gabrielsen, and Chastel, 2007). Taken together, these factors of food availability and other environmental changes may have a role in intra-pair conflict, as individuals are negotiating to brood the chick rather than to forage.

Allopreening and bill-fencing are common social behaviours observed during co-attendance. Allopreening, when a bird preens another bird's plumage (Harrison, 1965) may be an important element in communication, pair bond formation and maintenance. Allopreening may function as a reciprocal stress reducer (Kober and Gaston, 2003; Lewis et al., 2007) but it is not well understood (Lewis et al., 2007). Often, it has been described as related to ectoparasite removal (Barton, Harris, Wanless and Elston, 1996) or plumage maintenance and observed between pairs of socially bonded birds. Allopreening most often occurs in sexually monomorphic species (Harrison, 1965), such as murres. In some species, allopreening may also stimulate the production of the pituitary hormone prolactin which, in turn, promotes parental care (Buntin, 1986).

Although most previous research described bill-fencing as an aggressive display in male-male interactions (Ellis, 1966; Power, 1966; West, 1976; Baptista and Atwood, 1980), or in interactions between siblings (Anderson and Ricklefs, 1995) or strangers (Moynihan and Hall, 1954), bill-fencing also occurs between mated pairs during co-attendance (Harrison, 1965; Birkhead, 1978; Langmore and Bennett, 1999; Daniel, Millar, Ismar, Stephenson and Hauber, 2007). Individuals fence with their bills by

opening them in succession and then follow up with non-aggressive interactions (Garnetzke-Stollmann and Franck, 1991). Common murre bill-fencing has been described as a greeting when a partner returned to the nest site (Birkhead, 1978).

Variations from the regular nest relief sequence, as well as patterns of allopreening and bill-fencing, could provide a way to examine intra-pair interactions that may reflect negotiations. I investigated the differences in the proportions of various sequences (regular and variations from regular) during co-attendance. I also examined the changes in patterns of common co-attending behaviours (allopreening and bill-fencing) of brooders and returners in relation to different nest interaction sequences. Finally, I investigated allopreening and bill-fencing in relation to nest exchange interactions and individual quality as measured by CORT and body condition. I predicted that when a returner does not bring in a fish, it will have a different allopreening pattern (greater frequency and/or duration) than during a regular nest relief sequence. I expected the brooder to alternate its allopreening pattern and nest exchange behaviours depending on what the returner does (i.e., brings or does not bring a fish). I expected a higher proportion of non-provisioners (returners without fish) to depart, rather than exchange parental duties, as the brooder will be more likely to prevent a nest relief and remain at the nest site. I predicted that there is a relationship between body condition and behaviours based on the breeding bird's role; when it takes longer for the brooder to begin a nest relief, either if the returning partner is in good body condition or the returner is in poor body condition, it will stay after provisioning the chick. I predicted that there is a relationship between a breeder's CORT levels, body condition, and behaviours. Birds

with high CORT levels should have partners that will negotiate by beginning to allopreen sooner and for a longer duration. In addition, a bird in good body condition returning with a fish will depart the nest site more quickly to compensate for its partner.

2.3 METHODS

2.3.1 Field

2.3.1.1 Study site location

The study was conducted in 2009 on southeast point of Gull Island (47°16 'N, 52°46 'W; Figure 2.1) in the Witless Bay Ecological Reserve on the southeast coast of Newfoundland, Canada. Two observers recorded behaviours from inside and beside a one-man observation blind, located approximately 25 m from the study plot (Figure 2.2). The observations were conducted from June 27 to August 2 on 17 pairs of murres that had successfully hatched eggs (Figure 2.3). The breeding pairs were distinguishable by their location, by bands on at least one individual of the pair or by bridling (white eye-ring or spectacle and auricular groove behind eye morph confined to the murres of the Atlantic, Birkhead, 1984; Ainley et al., 2002).

Observers recorded individual behaviours (Table 2.1) using a camcorder or binoculars and a hand-held computer with behavioural research software. A *sequence* is defined as the series of behaviours beginning when a returning bird (hereafter, "returner") arrived and joined its partner that was brooding the chick (hereafter, "brooder") and ending when one of the pair departed.

A Canon VIXIA HF20 Dual Flash Memory Camcorder was used to record individual interactions intra-pairs. Up to 6 h per day of observations were recorded from June 27 to August 2 2009 for a total of 35 days of observations. Recordings were conducted alternating between mornings which began at about 0530h and afternoons-evenings which began at about 1430h. Recording times were alternated to capture sequences during different times of day. The maximum recording time was 6 h (constrained by battery life). In addition, seven all-day behavioural watches were conducted (approximately 0500-2100h). The camcorder was operated by one observer from inside the blind. The zooming capacities of the camcorder enabled the observer to record one of five groups of pairs in one frame but not the entire study plot at a given time (Figure 2.4). As such, more than one sequence could be recorded at one time at adjacent nest-sites.

The second observer, located outside of the blind, recorded behaviours on a hand-held computer (Noldus) using behavioural research software (Noldus Information Technology, Wageningen, The Netherlands). The Noldus Information Technology Pocket Observer^{TM} 2.0 (2005) software program on a PSION Teklogix Workabout Pro Hand-held computer C Version (2007) was used to record the timing of arrivals, departures, nest reliefs and chick feeding behaviours and information about prey items. This second device was used because the camcorder could not capture all of the pairs in one frame and also to try another method of recording behavioural data. Care was taken to ensure that the two observers were recording different pairs, except for 7 sequences later used to compare data taken by the two methods (June 27, July 2, 18, 21 and 23). A

coding scheme was set up to be able to follow one pair during co-attendance. It included behaviours (Table 2.2) created on the Noldus Information Technology The Observer® XT (2007) software program and used with the Noldus Information Technology Pocket Observer™ 2.0 (2005).

2.3.2 Data extraction

The recordings on the camcorder were automatically divided into ~20 min increments by the camera software and each segment was stitched together to allow for continuous viewing. In addition, the format was changed from the Advanced Video Codec High Definition (AVCHD; file extension of *.mts) to a video file format (file extension of *.m4v) to be compatible with the logger application (© A. Earle, 2007). The logger application is an event recorder designed for recordings played in QuickTime and was used to code all the behaviours occurring in marked pairs. In total, 248 behavioural sequences (62.04 h; Table 2.3) were recorded with the camcorder. The information collected on the Noldus Information Technology Pocket Observer™ 2.0 (2005) software was extracted using the Noldus Information Technology The Observer® XT (2007) software program. The durations and counts of behaviours were extracted using the software program to match the information extracted from the analysis of the camcorder recordings. In total, 65 behavioural sequences (17.38 h) were recorded with the Noldus (Table 2.3). Allopreening was quantified as a single action which began when the preener's bill had contact with its partner and ended with its withdrawal. These behaviours were noted on the Noldus as either single or grouped actions representing

bouts of allopreening (1-3, 3-6, and 7-10 bouts) and were averaged as 2, 5 and 8 bouts respectively to allow for comparison with the camcorder data.

2.3.3 Blood Sampling

Adult birds were caught with a noose pole (modified fishing pole) when the chicks were about 10 days old. Twenty-two birds were captured on July 9 and 15, from 0630-0900h. Handling of the birds was completed within 3 min of capture in order to obtain unstressed or baseline CORT levels (Romero and Reed, 2005). Once a bird was caught, it was placed head first in a cotton bag and approximately 1.5 mL blood sample (2 cc) was taken from the brachial wing vein using a 23-gauge butterfly needle attached to a $3cm^3$ syringe (Doody et al., 2008). Then, two bands were placed on each leg with a unique combination of three colour Darvic© bands and a triangular Canadian Wildlife Service metal band. The bird was then weighed with a 1000 g or 2500 g spring scale to ± 10 g. The tarsus length was measured to ± 0.1 mm using sliding callipers (e.g. Hanners and Paton, 1985). Approximately half of the blood sample was dropped onto a blood spot card (Whatman® Human ID Bloodstain card BCF180) and the remainder was transferred into a 1.5 mL microcentrifuge tube and placed in a portable cooler with a warm water bottle to prevent clotting prior to centrifugation. The blood was centrifuged using a VWR® Galaxy 7D digital microcentrifuge (VWR®, West Chester, PA, USA) for approximately 10 min and the top layer (serum) was removed and stored in a separate 1.5 mL microcentrifuge tube for use in a separate lipid analysis. The serum was stored in a freezer (-20°C) on the same day to avoid hormone deterioration. The blood spot cards were air dried overnight and also stored at -20°C.

2.3.4 CORT and body condition in relation to behaviours

Behaviours that were observed nearest in time to the capture of the individual (within a range of ± 4 days) were used to correlate with an individual's CORT and body condition. Body condition was measured as the individual's mass (g) divided by the tarsus length (mm; Jakob, Marshall, and Uetz, 1996). Analyses of behaviours were conducted twice for each individual; once when the individuals was in the role of the brooder and then in the role of the returner.

2.3.5 Laboratory

Birds were sexed using total DNA purified from common murre whole blood amplified by PCR (*see* Appendices A, B and C). CORT was extracted from blood spot cards. The conversion of CORT (blood spot values to measurable hormone concentrations in serum values) was determined using the protocol outlined in Doody et al. (2008). For the process of extraction and analysis, the concentrations of CORT were established using the COAT-A-COUNT Rat Corticosterone ^{125}I radioimmunoassay kits (Cat. # TKRC1, Inter Medico, Markham, ON, Canada). Changes were made to the process outlined in the kit for both the blood spot and serum assays (following Doody et al., 2008). In setting up for the blood spot assay, 30 µL each of the 7 assay calibrators (0, 20, 50, 100, 200, 500 , 1000 or 2000 ng/mL) was repeatedly spotted onto the individually labelled blood spot cards (Whatman® Human ID Bloodstain card BCF180). These cards were then left overnight to air dry and stored at -20 °C. A 3.2 mm diameter circular hole punch was then used to punch out 24 paper circles from numerous spots of each of calibrator or unknown blood spot. Each set was labelled and separately bagged and kept

at -20 °C. Tubes were labelled to match the various calibrators, unknowns and control. For each matching antibody-coated tube, 12 paper circles of the proper calibrator or unknown were placed inside. To count total radioactivity, two uncoated tubes without paper circles were reserved. All samples were run as duplicates with two sets of 12 where possible, otherwise a singlicate was run. In the latter case, a blank tube was placed where the duplicate would have been when these were counted in a LKB 1278 Gammamaster five-welled gamma counter.

A conversion formula was developed using a linear regression formula (blood spot CORT range: 58.1–188.4 ng/ml; serum CORT range: 9.9–31.4 ng/ml) in order for the CORT results to be comparable with other studies that relate blood spot assay values to concentrations of hormones (Doody et al., 2008).

2.3.7 Behavioural Analyses

Differences in male and female provisioning rate during chick rearing were determined with a paired sample *t*-test (based on seven all-day behavioural watches). In addition, the proportions of irregular nest interaction sequences to the total number of nest sequences between the sexes (within pairs) were compared with a paired *t*-test.

To test for possible effects due to chick age and time of day, variables were categorized into early (1 to 10 days post hatch) and late (11 to 21+ days post hatch) and AM and PM. Proportions of regular versus irregular nest interaction sequences by time of day were determined with a Yates χ^2 test. The differences in co-attendance, those relating to behaviours (allopreening and bill-fencing) in the morning or afternoon and in

early or late chick age were determined with ANOVAs with separate analyses for fish and fishless sequences. The fixed factors were time of season and time of day and a particular behaviour or co-attendance time was the dependent variable.

When both birds were at the nest, a regular nest relief sequence could occur or a sequence could end in several ways categorized as irregular nest interaction sequences. Frequencies of behaviour during irregular nest interactions were compared with those in regular nest relief sequences with one-way ANOVAs. Significant ANOVAs were followed by Least Significant Difference (LSD) *post-hoc* tests to examine differences between the means. Irregular sequences were categorized as: i) provisioner leaves sequence- the returner brings a fish, then leaves (no exchange of brooding duties), ii) multiple nest relief fish sequence - multiple nest reliefs which culminate in the brooder or the returner departing as an exchange or no exchange of brooding duties, or iii) fishless sequence - when the returner fails to bring a fish. The last sequence type was not separated into time of day due to the small sample size (preliminary analysis showed that fishless sequences were behaviourally similar regardless of time of day). With the exception of fishless sequences, all other nest interaction sequences were grouped by time of day (AM and PM), because preliminary analysis indicated differences in chick feeding rates in the AM than the PM (Harris and Wanless, 1985). Burger and Piatt (1990) found that chick feeding rates on Gull Island were higher from dawn to 0800h compared to the mean rate on throughout the day. However, diurnal chick feeding rates remained relatively constant.

Differences in behaviours within individuals were compared by: i) fishless sequences versus fish sequences, ii) regular nest reliefs where no relief and multiple relief sequences made by the same individual closest to the date of capture (blood sampling and morphometric data collection). Paired *t*-tests were used to compare the differences in behaviours of the same individual in the AM and PM and when the individual was brooder or returner in different sequence types.

CORT level (high or low) was compared to time taken to begin allopreening (latency) using an independent *t*-test. Also, CORT and body condition were compared to the two sampling dates (July 9 and July 15) using an independent *t*-test. Next, body condition of the returners and brooders were compared to various behaviours exhibited at the nest site and sequence types using Pearson correlations. Finally, the relationship of CORT and body condition was compared with the proportion of regular nest relief interactions, and irregular nest interactions using a Pearson correlation. All statistical analyses were conducted using SPSS 18.0 (SPSS Inc., 2009) with a significance level of $\alpha = 0.05$. Results are presented as mean ± SE unless otherwise specified.

2.4 RESULTS

2.4.1 Provisioning behaviour

There was no difference in the daily provisioning rate by males (1.62 ± 0.17 fish per day) or females (1.79 ± 0.20 fish per day; $N = 12$, $t = -0.72$, $p = 0.49$).

2.4.2 Behavioural analyses of nest interaction sequences

There was no significant difference in the proportion of all irregular nest interaction sequences to the total number of all nest sequences by males (0.44 ± 0.05 fish per day) or females (0.48 ± 0.05 fish per day; $N = 15$, $t = 0.47$, $p = 0.64$).

The proportion of regular nest relief sequences per total observations for each pair was 0.53 ± 0.11SD. There were no differences in the proportion of regular nest relief sequences compared to irregular nest interaction sequences in the AM or PM ($\chi^2 = 0.68$, $df = 1$, $p = 0.41$). During fish sequences, pairs spent more time together and took longer to exchange brooding duties (longer latency to first nest relief) in the PM than in the AM (Table 2.4). Also, for fish sequences, pairs bill fenced more often and both returners and brooders allopreened more often in the PM than in the AM (Table 2.4). All other behaviours during fish sequences were not significantly different between the two periods. During fishless sequences, time of day effects were not as apparent; the only significant behavioural difference was there were significantly more brooder allopreening bouts in the PM compared to the AM (Table 2.5).

During fish sequences, pairs engaged in more bouts of allopreening and bill-fencing during early rather than later chick age. Also, for fish sequences, the rate of returner's allopreening was higher when chicks were younger (Table 2.6). All other behaviours during sequences with fish were not significantly different between the two chick age categories. For fishless sequences, only the pairs' bill-fencing rate was significantly higher in late rather than early chick age (Table 2.7). Subsequent data

analysis involved the separation of sequences into AM and PM based on the information above for the fish sequences because more behaviours differed by time of day than by chick age. The exception is the fishless sequence category, because the number of sequences when separated by time of day (N_{AM} = 11; N_{PM} = 19) were low, and time of day differences were minimal. Thus, all further analyses were performed on the combined (AM and PM) fishless sequences.

2.4.3 Differences between various sequence types and behaviours at the nest site

Behavioural differences were most pronounced in the AM, so I will concentrate on these analyses and only discuss the PM data where I found differences in behaviour among sequence types.

2.4.3.1 Co-attendance time

Pairs spent significantly less time together during regular nest relief sequences than both fishless sequences (LSD *post-hoc* test: $p < 0.001$) and multiple nest relief fish sequences (LSD *post-hoc* test: $p = 0.03$, following significant ANOVA, $F_{3,195} = 9.61$, $p < 0.001$; Table 2.8). Significantly less time together was also spent in sequences when the provisioner leaves as compared to both fishless sequences (LSD *post-hoc* test: $p < 0.001$) and multiple nest relief fish sequences (LSD *post-hoc* test: $p = 0.03$; Table 2.8).

2.4.3.2 Latency to first nest relief

Latency to completion of the first nest relief differed significantly across sequence types in the AM ($F_{3,145} = 9.87$, $p < 0.001$; Table 2.8). Nest reliefs in fishless sequences

occurred more slowly than in regular nest relief sequence (LSD *post-hoc* test: $p = 0.005$) and in comparison to the first nest relief in multiple nest relief fish sequences (LSD *post-hoc* test: $p = 0.015$; *see section* 2.4.3.1). There were no differences to the completion of the first nest relief between regular nest relief sequence and multiple nest relief fish sequences. Finally, nest reliefs occurred more quickly in multiple nest relief fish sequences than in fishless sequences (*see section* 2.4.3.1).

2.4.3.3 Allopreening rates and timing

The number of allopreening bouts ($F_{3,195} = 5.08$, $p = 0.002$) and allopreening rates ($F_{3,195} = 3.76$, $p = 0.01$) by returners differed between the various sequence types they performed in the AM. Returners performed significantly more allopreening bouts in fishless sequences than in regular nest relief sequences (LSD *post-hoc* test: $p < 0.001$), multiple nest relief fish sequences (LSD *post-hoc* test: $p = 0.01$) and sequences when the provisioner leaves (LSD *post-hoc* test: $p = 0.003$). Similarly, returners allopreened at a higher rate in the fishless sequences than in regular nest relief sequences (LSD *post-hoc* test: $p = 0.002$) and multiple nest relief fish sequences (LSD *post-hoc* test: $p = 0.02$; Table 2.9). Also, returners that subsequently left the nest site after bringing in a fish allopreened at a higher rate than during a regular nest relief sequence (LSD *post-hoc* test: $p = 0.03$; Table 2.9).

Consistent with these sequence type differences in allopreening rates, murres returning without a fish (fishless sequences) started to allopreen more quickly than in multiple nest relief fish sequences (LSD *post-hoc* test: $p < 0.001$ following significant

ANOVA, $F_{3,195} = 7.25, p < 0.001$; Table 2.9). In addition, returners started allopreening significantly sooner in the AM during both regular nest relief sequences (LSD *post-hoc* test: $p < 0.001$) and sequences when the provisioner leaves (LSD *post-hoc* test: $p = 0.001$) than in multiple nest relief fish sequences (Table 2.9). In the afternoon, returners took significantly less time to begin allopreening their partners during fishless sequences compared to regular nest relief sequences (LSD *post-hoc* test: $p = 0.03$), sequences when the provisioner leaves (LSD *post-hoc* test: $p = 0.01$) and multiple nest relief fish sequences (LSD *post-hoc* test: $p = 0.02$; Table 2.9).

Brooders in the various sequence types differed in the number of allopreening bouts ($F_{3,145} = 4.27$, p = 0.006) and in their allopreening rates ($F_{3,195}$ 4.24, $p = 0.006$) in the AM. Generally, brooding murres allopreened less often and at a lower rate in sequences when the provisioner leaves without a nest relief than in the other sequence types. Specifically, murres allopreened less often in sequences when the provisioner leaves than in fishless sequences (LSD *post-hoc* test: $p = 0.01$), multiple nest relief fish sequences (LSD *post-hoc* test: $p = 0.001$) and regular nest relief sequences (LSD *post-hoc* test: $p = 0.02$; Table 2.9). Brooding murres also allopreened less during regular nest relief sequences than in multiple nest relief fish sequences (LSD *post-hoc* test: $p = 0.01$, Table 2.9). Brooders allopreened at a significantly lower rate during sequences when the provisioner leaves than during regular nest relief sequences (LSD *post-hoc* test: $p < 0.001$) and multiple nest relief fish sequences (LSD *post-hoc* test: $p = 0.01$; Table 2.9) in the AM. Finally, brooders began allopreening their returning partners significantly sooner in regular nest relief sequences compared to sequences when the provisioner

leaves (LSD *post-hoc* test: $p = 0.05$; Table 2.9). In the PM, brooding murres allopreened significantly more in multiple nest relief fish sequences compared to regular nest relief sequences (LSD *post-hoc* test: $p = 0.02$), sequences where the provisioner leaves (LSD *post-hoc* test: $p = 0.01$) and fishless sequences (LSD *post-hoc* test: $p = 0.01$, Table 2.9).

Returners and brooders in regular nest relief sequences did not differ from each other in frequencies, rates or latencies to allopreen (Figure 2.5, Figure 2.6 and Figure 2.7). Similarly, there were no differences in any allopreening measures related to initial brooder or returner role during multiple nest relief fish sequences where brooder and non-brooder statuses change throughout the interaction. In contrast, returners in fishless sequences started allopreening sooner after they arrived ($t = -3.48$, $df = 29$, $p = 0.002$; Figure 2.7) and allopreened at a significantly higher rate than brooders ($t = 2.86$, $df = 29$, $p = 0.008$; Figure 2.6). Similarly, brooders in sequences when the provisioner leaves exhibited fewer allopreening bouts ($t = 4.64$, $df = 41$, $p < 0.001$; Figure 2.5), had a lower allopreening rate ($t = 4.97$, $df = 41$, $p < 0.001$; Figure 2.6) and took longer to start allopreening than their arriving partners ($t = -4.09$, $df = 41$, $p < 0.001$; Figure 2.7).

2.4.3.4 Bill-fencing bouts, rates and latency

There were no differences in bouts, rates or latencies to bill-fencing in the AM (Table 2.8). During PM observations, murres performed significantly more bill-fencing bouts in multiple nest relief fish sequences compared to every other sequence type (ANOVA, $F_{3,140} = 5.05$, $p = 0.002$, regular nest relief sequence: LSD *post-hoc* test: $p =$

0.001; sequences when the provisioner leaves: LSD *post-hoc* test: $p = 0.005$; fishless sequence: LSD *post-hoc* test: $p < 0.001$; Table 2.8) .

2.4.3.5 Matched fishless and fish sequences (regular nest relief sequences only) at the individual level

Consistent with the overall data, the returners' allopreening rates were significantly greater when they did not bring a fish compared to when the same birds brought one ($t = -2.40$, $df = 14$, $p = 0.02$; Figure 2.8). Brooders' allopreening rates also did not differ significantly for fishless sequences and regular nest relief sequences ($t = 0.09$, $df = 14$, $p = 0.47$; Figure 2.8).

2.4.3.6 Matched regular nest relief sequence with no nest relief and multiple nest relief sequences at the individual level

Brooders allopreened at a significantly lower rate during sequences without a nest relief compared to regular nest relief sequences ($t = 2.11$, $df = 23$, $p = 0.02$; Table 2.10; Figure 2.8). Co-attendance time was significantly higher during multiple nest reliefs compared to regular nest relief sequences ($t = -2.71$, $df = 29$, $p = 0.01$; Table 2.10). Returners' latency to allopreen was significantly higher for multiple nest relief fish sequences compared to regular nest relief sequences ($t = -2.00$, $df = 29$, $p = 0.03$, one-tailed; Table 2.10). Also, latency to first nest relief was significantly higher for regular nest relief sequences compared to multiple nest relief fish sequences ($t = 4.74$, $df = 29$, $p < 0.001$; Table 2.10). Finally, the number of bouts of bill-fencing for multiple nest relief fish sequences was significantly higher compared to regular nest relief sequences ($t = -2.55$, $df = 29$, $p = 0.01$; Table 2.10). This pattern of significant results for matched sequences duplicates the findings using the overall data.

2.4.4 Latencies to allopreening in relation to CORT

Returners (t = -1.89, df = 13, p = 0.05; Table 2.11) and brooders (t = -1.77, df = 13, p = 0.05; Table 2.11) with high CORT had significantly greater latencies to allopreening compared to those with low CORT. Also, CORT was higher for birds sampled on the earlier of the two sampling dates (July 9 and 15, (t = 1.89, df = 13, p = 0.04 one-tailed) 2009; Table 2.12), indicating that CORT decreased over this period.

2.4.5 Nest relief sequences in relation to body condition.

Brooders with partners in good condition delayed the start of nest reliefs (latency to first nest relief was longer; Pearson r = 0.47, N = 14, p = 0.04, one-tailed) and had a higher proportion of sequences when the provisioning partner left without switching duties (AM and PM combined: Pearson r = 0.51, N = 14, p = 0.03, one-tailed). Also, brooders in better body condition had a lower proportion of regular nest relief sequences than brooders in poorer condition (Pearson r = -0.53, N = 14, p = 0.03, one-tailed). Finally, body condition was better for birds sampled on the earlier of the two sampling dates (July 9 and 15, 2009; t = 2.93, df = 13, p = 0.015; Table 2.12), indicating that body condition declined during this portion of the chick-rearing period of the breeding season. In summary, returners in better body condition were more likely to depart after chick provisioning whereas brooders in better body condition had more irregular nest interactions where either returners were not allowed to brood or did not bring in a fish and/or the brooder remained at the nest site.

2.5 DISCUSSION

2.5.1 Negotiation behaviour in various sequence types

Research on seabirds suggests that nest reliefs and nest relief ceremonies during co-attendance are an important part of intra-pair communication (Müller-Schwarze and Müller-Schwarze, 1980; Niebuhr and McFarland, 1983). Allopreening and bill-fencing differed among the sequence types. Attempts to delay the nest relief, attempted nest reliefs without first provisioning the chick, and associated behaviours may constitute negotiation within the pair. In addition, behaviours such as when a bird delivers a fish and departs may constitute a non-negotiable behaviour. The bird may be "aware" of a capelin school to revisit. The role of the individual may influence the amount of allopreening used as a part of negotiation and might agree with Lewis et al. (2007), who found no evidence for reciprocity in murre intra-pair allopreening rates. Returners allopreened more in fishless sequences and brooders allopreened less often in sequences in which the provisioner departed without an exchange of parental duties. An interpretation may be that returners negotiate by not bringing in a fish and then allopreening at a higher frequency in order to take over brooding duties, but this negotiation is not accepted. Brooders negotiate by reducing allopreening and not allowing the provisioner to exchange parental duties. Also, the brooders successfully negotiate in a multiple nest relief fish sequence by remaining at the nest after an odd number of nest reliefs; a negotiation that the returner accepts by departing. During multiple nest relief fish sequences, allopreening by the former brooder usually occurs after the first nest relief. The former brooder's behaviour could indicate that it is trying to

"encourage" the partner to allow a subsequent nest relief which would allow the former brooder to remain at the nest. Also, bill-fencing may be an escalated behaviour that occurs if allopreening alone is not effective in communication. The most frequent bill-fencing occurred during multiple nest relief fish sequences. In summary, lack of brooder allopreening, the returner arriving without a fish, a returner's high frequency of allopreening during fishless sequences, and the brooder not exchanging brooding duties can be considered to constitute negotiation behaviours.

Generally, frequency and duration of several behaviours differed during various sequence types in the AM and the PM. Nest reliefs occurred more quickly in the morning than later in the day. The proportion of irregular nest interactions to regular nest relief sequences did not differ in either the AM or the PM. For fish sequences in the PM, pairs spent more time together, took longer to exchange brooding duties, and had higher rates of intra-pair bill-fencing and allopreening. The negotiation patterns may be attributed to lower prey accessibility in the PM when foraging may be less worthwhile due to lower capelin availability (Regular, Davoren, Hedd and Montevecchi, 2010). Latencies to first nest relief during a regular nest relief took significantly longer in the PM than in the AM but former brooders also stayed longer at the nest after exchanging duties in the PM. Therefore, more negotiating for the brooding role occurs in the PM as it approached the overnight foraging shift (Regular et al., 2010) than in the AM, and this may relate to the higher incidence of bill-fencing which may also be used in negotiation.

However, most of the behavioural differences between sequence types occurred in the AM, and it may be during this time of day that the use of different negotiation

strategies is most important. This may be because there was more conflict in the AM, as individuals were less responsive to the other's communicative efforts. Harris and Wanless (1985) found a peak in chick feeding in the early morning. As well, other studies report that there are more behavioural interactions and provisioning trips earlier on in the day for murres (Burger and Piatt, 1990; Davoren, 2001); time of day differences in provisioning were not investigated in this study. However, it may be plausible that there would be more opportunities for sequence variability in the morning because of the greater number of provisioning trips (Burger and Piatt, 1990; Davoren, 2001). In the current study, slower nest reliefs may be related to higher frequencies of bill-fencing because allopreening alone was not enough to facilitate the start of an exchange of brooding duties.

Intra-pair negotiation behaviours were involved in the delay or prevention of the exchange of brooding duties. It appears that the returner in fishless sequences and the brooder in multiple nest relief fish sequences and in sequences where the provisioner leaves without brooding were negotiating to stay longer at the nest compared to the significantly shorter co-attendance time during regular nest reliefs. Staying at the nest is less energetically taxing than provisioning (Croll and McLaren, 1993), and some birds might be trying harder to stay in the brooder role. Brooders in better body condition negotiated to stay at the nest site during nest reliefs in which the returner eventually departed.

During multiple nest relief fish sequence, it is likely that more time was spent negotiating brooding duties than during a regular nest relief sequence (only one exchange

of brooding duties) because there was more than one nest relief, indicating conflict over brooding duties. It could also be that there is less negotiation if the first nest relief happens more quickly after the arrival of the returner. Negotiation in this sequence type would be when the former brooder does not leave after the first nest relief and both birds negotiate to stay. Conversely, a brooder that does not negotiate would depart after the first nest relief and a regular nest relief sequence would result. This back and forth exchange of brooding duties in a multiple nest relief fish sequence suggests that both birds are in conflict about which will remain at the nest site. The returner either accepted the negotiation by leaving or did not accept by remaining and brooding the chick (*see* Table 3.3), both behaviour patterns which occurred equally. The latter outcome would constitute a successful negotiation on the part of the brooder.

During a fishless sequence, returners increased allopreening, presumably to negotiate taking over brooding duties. Conversely, during the "provisioner leaves" sequence, brooders lowered their amount of allopreening to negotiate to remain at the nest. It is possible that fewer allopreening bouts by the brooder signified that it was negotiating by not engaging in a "regular" pattern of interaction, while more allopreening by the returner signified it was negotiating to take over brooding duties. The results indicate that during a regular nest relief sequence, the amount of allopreening by both the brooder and returner is the same; allopreening is mutually reciprocated. However, during a sequence in which the provisioner leaves, the brooder usually does not reciprocate the allopreening of its mate. The returner accepts the brooder negotiation and goes back to sea to forage and provision the chick without having a brooding bout.

Returners negotiate by increasing their allopreening rate and brooders negotiate by decreasing it. When birds attempt to stay at the nest site after returning, they do so by increasing the amount of allopreening as a negotiation strategy. Conversely, brooders that attempt to stay at the nest site longer negotiate by lowering the amount of allopreening. These differences support the view of allopreening as a behaviour that serves as an important social function in colonial socially monogamous species (Lewis et al., 2007). Common murre intra-pair allopreening rate was associated with long-term fitness (Lewis et al., 2007). Although Lewis et al. (2007) did not find evidence that allopreening was important in maintaining the pair bond, it may still be an honest signal of quality, important in mate choice (Roberts, 1998). This study may indicate that allopreening functions as negotiation tool in addition to reaffirming a pair bond after a period of separation (Black, 1996 as cited in Lewis et al., 2007).

In fish sequences, bill-fencing occurs more in the PM when nest reliefs are longer. There were a significantly greater number of bill-fencing bouts in the PM during fish sequences, which suggests that this aggressive display (Harrison, 1965; Birkhead, 1978) was shown more often during longer co-attendance times. More specifically, the greater number of bill-fencing bouts during multiple nest relief fish sequences compared to all other sequence types (PM) suggests that individuals in the pair were communicating to solicit the other to conduct a nest relief and have the partner subsequently depart. The average rate and latency of bill-fencing was not significantly different with respect to time of day. Bill-fencing may be higher during multiple nest relief fish sequences because there is a greater conflict between the individuals in the pair to negotiate which

bird will brood the chick. Therefore, the interactive negotiation strategies of bill-fencing, and, to a greater extent, allopreening, may be communication tools for one individual to relay information about its own self-interests to its partner.

Comparisons of all recorded sequences and matched comparisons at the individual level were made to determine if there were consistent behavioural patterns when individuals were involved in various nest interaction sequences. All significant differences were consistent between the two groupings of sequences (all recorded sequences matched at the individual level), and provides strong support for the importance of these behavioural sequences in negotiation.

Some other factors that could not be examined in this particular study was the effect of age on parental care (Torres, Drummond, Velando, 2011) as well as pair bond duration in relation to individual behaviours. These potential factors could be studied in accessible colonies that have identifiable pairs that can been monitored for a number of consecutive years. Sundberg, Kadin, Olsson and Österblom (2010) have created an artificial breeding ledge for common murres. The ledge can be outfitted with automatic balances, video surveillance and antennas for Passive Integrated Transponder-tag readers (Hentati -Sundberg, Österblom, Kadin, Janson & Olson, 2011).

2.5.1.1 Chick growth

Co-attendance time and the associated behaviours changed over the chick rearing period. Both brooders and returners allopreened and bill-fenced less often and co-attendance time was shorter later in chick-rearing compared to earlier. Hipfner, Gaston

and Smith (2006) found that parents provisioned at higher rates because of increased food intake requirements of older thick-billed murre (*Uria lomvia*) chicks over the season. Therefore, increased chick energetic requirements could be a reason why parents spent less time together on Gull Island in late chick-rearing.

2.5.2 Nest-site interactions in relation to CORT and body condition

In birds, as a response to an apparent stressor, the adrenal cortex increases the circulating levels of glucocorticoid hormones via the hypothalamic-pituitary-adrenal cascade (Wingfield et al., 1998; MacDougall-Shackleton, Dindia, Newman, Potvin, Stewart and MacDougall-Shackleton, 2009). Studies on wild and captive birds indicate that CORT (synthesized from cholesterol) is the primary glucocorticoid (Holmes and Phillips, 1976 cited in Remage-Healey and Romero, 2002). CORT, referred often as a "stress" hormone and the primary mediator of allostasis "maintaining stability through change, as a fundamental process through which organisms actively adjusts to both predictable and unpredictable events" (McEwen and Wingfield, 2003). An organism can cope during an "emergency" life history stage within minutes to hours with an increase in CORT (Wingfield et al., 1998). In birds, levels of stress hormone increase as food availability decreases (Kitaysky et al., 1999; Vleck et al., 2000; Clinchy et al., 2004). Due to the lack of inshore spawning of capelin in nearby Ferryland (B. Nakashima, Canadian Department of Fisheries & Oceans [DFO], pers. comm.), CORT levels might have been high in response to low prey availability.

Doody et al. (2008) found a relationship between baseline CORT levels of breeding murres, provisioning and capelin inshore arrival date. During a year when inshore spawning of capelin occurred after the onset of chick hatching (prey mismatch year), birds with higher CORT had above average chick feeding rates than birds that fed their chicks at lower than average rate during the same time period. Conversely, during a year when the arrival of capelin matched timing of chick hatching (prey match year) , birds with higher CORT provisioned less than birds with lower CORT, possibly to induce partners to compensate by increasing foraging rates (Storey et al., 2009). Provisioning was not investigated in relation to CORT but was compared to food availability separately (*see section* 3.4.1). Based on Doody et al. (2008) and the lack of inshore spawning of capelin as observed in nearby Ferryland (B. Nakashima, Canadian Department of Fisheries & Oceans [DFO], pers. comm.), it may be a reasonable assumption that birds on Gull Island with higher CORT might have provisioned even more than those with lower CORT to solicit compensation with an increase in foraging rates, but only to a certain threshold (*see* Chapter 1; Jones et al., 2002).

In general, pairs with higher CORT had less efficient co-attendance interactions. Focal brooding murres with high CORT delayed allopreening with its returning partner indicating that it attempted to brood more. Also, murre pairs in which one individual had high CORT spent more time together at the nest site and may have taken longer to begin bill-fencing. Finally, latency to first nest relief did not differ in pairs in which one individual had high CORT. Overall, the levels of CORT are the effect of inefficient nest

interactions and/or food availability. Therefore, an individual's stress level may decrease the amount of social interactions within a pair.

CORT levels and body condition were significantly higher on July 9 compared to birds sampled almost a week later on July 15. Doody et al. (2008) found that birds sampled earlier in the chick-rearing period had higher CORT levels in a prey mismatch year, which implies that baseline CORT was higher when there was low prey availability. In thick-billed and common murres, body mass was found to decline during chick rearing (Croll, Gaston and Noble, 1991; Wilhelm et al., 2008), and was related to lower prey availability (Wilhelm et al., 2004). Earlier in the breeding season, birds had greater stress levels and poorer body condition, which could be due to the lack of inshore spawning of capelin in nearby Ferryland (B. Nakashima, Canadian Department of Fisheries & Oceans [DFO], pers. comm.) and the greater number of breeding birds with chicks that would be required to forage during this time. However, since sampling was conducted twice during a small portion of the chick rearing period, it might not be accurate to forecast a declining trend for both body condition and CORT for the entire breeding season.

Based on the results of this study, common murres in poorer body condition negotiated and were compensated for by their partners in good body condition. Returners in good condition compensated for their partner by waiting longer for a nest relief than those in poorer condition, which supports the predictions of the Jones et al. (2002) model. Also, returners in good condition had more sequences in which they left without a nest relief and, therefore, were considered to be compensating for their partners by leaving the nest site after chick provisioning. In other words, birds in better body condition were

more likely to accept their brooding partner's negotiation to remain the brooder, compared to returners in poorer body condition. Brooders in poorer body condition had a higher proportion of regular nest relief sequences than brooders in better body condition, suggesting that they more often departed to self-feed and improve body condition first before possibly foraging for the chick. Successful reproduction is dependent on the mutual interest of maintaining a partners' body condition (Jones et al., 2002). The "graphical model" proposed by Jones et al. (2002), whereby decreasing parental effort could be a way for one parent to compensate for decreased parental effort by increasing the partner's parental care duties, would support the observations above.

2.5.3 Sequences recorded with two recording methods and best recording method for future behavioural observational work

See Appendices D, E and F for the comparison of data collection with the camcorder and Noldus. Duration behaviours such as co-attendance time could be measured with both the camcorder (on the Logger program) and Noldus. As these behaviours have a distinct onset, the observer could record the start of co-attendance and would have time to record the end of each sequence. Thus, recording of co-attendance times and the latency to onset of particular behaviours were comparable between the two methods.

Conversely, behaviours of short duration, such as bouts of allopreening, were more difficult to measure with the Noldus, especially when the observer was at a considerable distance. Therefore, the camcorder was superior for this and other

behaviours that were short in duration, repetitive and occurred in quick succession. Although behaviours of longer duration with a distinctive start and end point were recorded similarly on both recording devices, the camcorder (with the Logger program) was a better method overall for recording and analysing behaviours than the hand-held Noldus. Also, the details as seen from the distance of observer to the study plot with binoculars in the field was not as clear as a video clip viewed on a large desktop computer monitor. Details that could be missed included the often subtle and brief allopreening and bill-fencing behaviours. If a particular behaviour was difficult to observe in real time, the behaviours could be viewed again in slow motion and/or repeatedly. It was often a challenge to determine whether a bird brought a fish when seen live but with video data, it was possible to watch the sequence over again. Although much more post field season work was required to view and code the behaviours from video than from Noldus, ultimately it allowed for more accurate measurements.

There were also several advantages to the Noldus. The PSION Teklogix Workabout Pro Hand-held computer C Version (2007) was portable, water-resistant and the Noldus software was installed on the Windows operating system. Also, the view of the camcorder was best placed in a high density area of the plot where marked breeding pairs maximized recordings of sequences. The Noldus was then used for observations in an area of the plot where only one or a couple of pairs could be viewed. The main advantage was that the Noldus required much less post field season labour for data extraction. Unfortunately, the Noldus Information Technology Pocket Observer™ 2.0 (2005) used was not as powerful as the Noldus Information Technology The Observer®

XT (2007) software program installed on a desktop computer. The Observer® XT had to extract the data collected on the Pocket Observer™ 2.0, which could only be set up to code the behaviours of one pair at a time. In addition, due to the distance of approximately 25 m between the blind and the study plot, the recorder had to re-focus the binoculars on the recorded pair after behaviour was coded. The lag time between these activities would increase the chances of missed behaviours, inaccurate start or end time and/or number of bouts.

Future behavioural observational work where the study site is at a distance similar to this field site may benefit from using a camcorder in combination with an event recorder program rather than an on-site event recorder. Elliot, Davoren and Gaston (2008) found that the factors of greater distance, higher food delivery rates during midday and low levels of light led to a greater chance of missed feedings and/or misidentified prey species of the provisioning behaviour of thick-billed murres. Their range of distances between observers and the murres were 1 to 5 m whereas the distance was much greater in this study.

2.6 CONCLUSION

In this study I found that brooding common murres negotiated to stay at the nest longer by decreasing their allopreening rate and increasing the latency to this behaviour. Returners negotiated by increasing the allopreening rate when they did not bring in a fish compared to when they did deliver a fish. Communication appears to be occurring between individuals within the pair in the form of the length of co-attendance time,

allopreening, and bill-fencing, in which each behaviour might signal different levels of communication, as well as the timing and number of nest reliefs. Both CORT and body condition were related to negotiation and compensation behaviours at the nest site during co-attendance. Returners and brooders with higher CORT began allopreening later indicating that "stressed" individuals delayed interacting with their partner and were therefore allowing the brooder to brood longer. In general, pairs with higher CORT had less efficient co-attendance times, whereby the exchange or non-exchange of brooding duties was delayed. Stress levels may influence when to begin interactive behaviours regardless of the parental care role. This study supports the idea that parental interactions at the nest during co-attendance may involve pair members communicating their physiological status and negotiating behavioural duties in their own self-interest of current and potential future reproductive success.

2.7 RECORDING DEVICES

The camcorder and the event recorder program were the best combination of devices for detailed behavioural observations analyzed in this study site. With the Noldus, behaviours such as the number of bouts of allopreening were not recorded as accurately as with the camcorder recordings. Although the camcorder required more labour post-fieldwork, the end result was more detailed behavioural data. The camcorder can also be used as a validation tool for traditional visual observations on common murre provisioning rates (Newell, Harris, Wanless and Daunt, 2011).

2.8 LITERATURE CITED